H1.3. Spatiotemporal patterns in ectomycorrhizal populations

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Abstract: To understand the functioning and ecological roles of ectomycorrhizal fungi in natural ecosystems, it is necessary to have adequate knowledge of the spatial distribution of individual mycelial systems in populations and communities and how this distribution may persist or vary with time. However, this issue has attracted relatively little attention until recently. Moreover, the limited information available is mostly based on the distribution of sporocarps, which is at best an unreliable indicator of the location and activity of mycelia. More useful information can be obtained using somatic and sexual incompatibility tests, as well as molecular markers to trace the distribution of individual genets over a range of spatial and temporal scales. For example, it has been possible using this approach to demonstrate that while young populations tend to consist of numerous small mycelia, individuals in older populations tend to be fewer and larger but heterogeneous in scale. It has also been possible to verify the persistence over several years of mycorrhizal mycelial individuals. Such findings represent only the first step in the study of the spatiotemporal dynamics of ectomycorrhizal fungi, which promises to be a rich and important field for future research. Concepts concerning the process and mechanisms likely to affect distribution patterns are discussed.

Key words: ectomycorrhiza, population structure, population dynamics, spatiotemporal patterns.

Résumé : Pour comprendre le fonctionnement et les rôles écologiques des champignons ectomycorhiziens dans les écosystèmes naturels, il est nécessaire de disposer de connaissances adéquates sur la distribution spatiale des systèmes mycéliens individuels dans les populations et les communautés, et comment cette distribution peut persister ou varier avec le temps. Cependant, cette question n'a pas reçu beaucoup d'attention jusqu'ici. De plus, le peu d'information qui existe est surtout basé sur la distribution des sporocarpes, laquelle est à son meilleur un indicateur peu fiable de la localisation et de l'activité du mycélium. On peut obtenir plus d'informations utiles en utilisant les essais d'incompatibilité somatique et sexuelle ainsi que les marqueurs moléculaires, pour retraçer la distribution des clones individuels, sur un ensemble d'échelles spatiales et temporelles. Par exemple en utilisant cette avenue, on peut démontrer que bien que les jeunes populations tendent à regrouper des thalles nombreux et de petites dimensions, les individus des populations plus âgées ont tendance à être moins nombreux mais plus grands, mais à une échelle hétérogène. Il a également été possible de vérifier la persistence pendant plusieurs années de mycéliums mycorhiziens individuels. De telles constatations ne représentent que les premières étapes de l'étude de la dynamique spatio-temporelle des champignons ectomycorhiziens qui en font un champs de recherches futures des plus prometteurs. Les auteurs discutent les concepts concernant les processus et les mécanismes qui affectent vraisemblablement les patrons de distribution.

Mots clés : ectomycorhizes, structure des populations, dynamique des populations, patrons spatio-temporels. [Traduit par la rédaction]

Introduction

More than 5000 species of ectomycorrhizal (ECM) fungi have been described (Molina et al. 1992). In Sweden alone, over 800 species are known (Hallingbäck 1994) and the actual number present is probably about 1000. The ecological importance of these fungi is generally assumed to be profound but is difficult to assess without an adequate understanding of their population and community structure and dynamics.

So far, structural studies of communities and populations of ECM fungi have focused almost exclusively on sporocarps, with the implicit assumption that the production of these sporocarps reflects the amount of mycelial biomass and activity (Menge and Grand 1978; Bills et al. 1986; Arnolds 1991). Such assumptions may be valid for certain species, e.g., *Paxillus involutus* and *Russula ochroleuca* (Laiho 1970; Agerer 1990). However, recent studies indicate that the relationships between sporocarps and mycorrhizal production may vary between species, making interpretation difficult at the community level (Menge and Grand 1978; Lamb 1979; Danielson and Pruden 1989; Taylor and Alexander 1990; Gardes and Bruns 1993; M. Gardes and O. Kårén, personal communication). It is also likely that intraspecific relationships may change in response to variation in climatic and

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other environmental conditions and in response to succession in the fungal community.

In coniferous forests, ECM short roots and the extramatrical mycelia account for the predominant part of ECM fungal biomass and activity (Read 1991). Those nonreproductive structures are almost exclusively located in the humus (Mikola and Laiho 1962; Persson 1983). In boreal forest the mycelia are active for most of the year with dormancy being restricted to periods when the soil is frozen or the water potential is too low (Bååth and Söderström 1982; Cline et al. 1987; Coleman and Bledsoe 1989). Some ECM species may even be physiologically active at below-zero temperatures. Therefore, selection pressures on ECM fungi (such as intra- and inter-specific competition, grazing by fungivores, abiotic constraints, etc.) act predominantly on the mycorrhizas and mycelia. As a consequence, studies aimed at gaining an understanding of mycorrhizal fungal ecology must also consider these vegetative structures rather than concentrating solely on reproductive structures.

Good descriptions of the spatial structure at the mycelial level of mycorrhizal populations and communities are prerequisite for the accurate interpretation of ecological roles in terms of life history strategies and for predicting changes in distribution with time and the influence of various environmental factors. However, we fear that current knowledge of ECM ecology in natural ecosystems is biased for the following reasons. (*i*) Most studies have been based solely on the occurrence of sporocarps. (*ii*) Spatiotemporal population structures have been overlooked. (*iii*) Ecological concepts concerning ECM fungi have been based on studies of forests in primary rather than secondary stages of succession and centered more on the plant than on the fungus. (*iv*) Only a limited number of species and isolates have been studied in culture and field experiments.

Fungal individualism and the identification of genets

The inability to distinguish separate mycelia in nature has obscured the fact that many fungal species consist of physiologically and spatially discrete mycelial individuals (Todd and Rayner 1980; Dahlberg 1995). Such individuals can usefully be described adopting the terms genet and ramet, commonly used for vegetatively extending higher plants (Harper 1977). Genets are defined as all genetically identical mycelia, while ramets are offshoots derived by asexual or mycelial propagation (Brasier and Rayner 1987). Ramets can readily fuse by anastomosis. The term clones includes both genets and ramets and emphasizes the clonal propensity of fungi. In the following discussion we use the term population to describe an assembly of intraspecific genets. Populations can be delimited at various geographic levels (i.e., local to worldwide) depending on the purpose of the study. The fungal or ECM community is an abstraction at the interspecific level of the same kind as the population. An ECM fungal community simply consists of all fungal species occupying the area chosen for study.

It is generally not possible to spatially delimit genets of ECM fungi in the field by making sporocarp surveys or mapping mycelial distributions in excavation studies. The only fungi that can easily be approached in this way are those that form single-genet fairy rings and some of those forming dense mycelial mats in soil (Horn 1933; Cromack et al. 1979, 1988; Griffiths et al. 1991).

One way of analysing ECM communities has been to estimate the number of fruiting mycelia based on the occurrence of sporocarp aggregates (Haas 1932; Lange 1993 and references therein). The purpose has been to obtain data on individual mycelia rather than at the species level. However, the delimitation of genets based on the occurrence of sporocarps is arbitrary and difficult (Dahlberg 1991). In our studies of *S. bovinus* and *S. variegatus*, sporocarp aggregates of the same genets were sometimes located 10–25 m apart. At the same time, sporocarps from different genets could be located just a few decimetres apart (Dahlberg and Stenlid 1990, 1994; A. Dahlberg, unpublished data).

More commonly, ECM surveys register the numbers or biomass of sporocarps (see Arnolds 1991; Vogt et al. 1991). In such surveys sporocarp-producing species can be monitored and the production of sporocarp biomass calculated. Species or genets, not producing sporocarps or overlooked sporocarps, will inevitably be excluded from such studies.

If no physical boundaries can be distinguished, genetic markers are needed to delimit genotypes. To have the appropriate resolution, these markers must be sufficient in number, variability, or sensitivity. In the mid-1970s it became more generally realized that mycelial individuals can often be identified by their somatic (vegetative) incompatibility reactions (Rayner 1991), which prevent genetically different conspecific mycelia from integrating. In basidiomycetes, somatic incompatibility acts in the heterokaryotic phase and between homokaryons lacking complementary mating alleles. In ascomycetes, both somatic incompatibility and sexual compatibility act in the homokaryotic phase (Rayner et al. 1984). Mycelia within an ECM species coexist as discrete individuals maintaining their genetical integrity through territorial defence (Dahlberg and Stenlid 1990; Dahlberg 1995).

Somatic incompatibility, the very expression of fungal individualism that allows a mycelium to recognize and then accept or reject another depending on the degree of genetic disparity, offers a highly variable system and potentially valuable tool in the analysis of population structure and dynamics. However, the genetics of this system are often complex and vary between species (Brasier 1984; Hansen et al. 1993) so that it is important to do sufficient preliminary work on the variation-generating mechanisms in a particular population before deciding how reliable somatic incompatibility tests are in defining genets. Many saprotrophic fungi have been subjected to population structure analysis using somatic incompatibility tests (Kirby et al. 1990; Rayner 1991; Stenlid 1993; Leslie 1993). However, to our knowledge these tests have, so far, only been successfully applied to the ECM fungi *S. bovinus*, *S. variegatus*, *S. luteus*, *S. granulatus*, *Pisolithus arhizus*, and *Laccaria bicolor* (Fries 1987; Fries and Neumann 1990; Dahlberg and Stenlid 1990, 1994; and unpublished data; Sen 1990; Kopke 1992; Baar et al. 1994). Difficulties can arise because only a limited number of ECM species grow in culture and some species give indistinct and inconsistent reactions on agar plates (Dahlberg 1995 and personal observation; Jacobson et al. 1993; S. Miller and T. Bruns, personal communication).

Although mating types have frequently been used for delimiting intersterile groups or sibling species of wood decay fungi, this technique was not adopted for ECM fungi until recently (e.g., Fries and Neumann 1990; Fries 1994). Mating types have also been used for mapping the distribution of fungal individuals (Anderson et al. 1979; Chase and Ullrich 1983; Kile 1983; and others), but again work with ECM fungi has been limited (Buschena et al. 1992; de la Bastide et al. 1994).

The use of random amplified polymorphic DNA (RAPD), if adequately controlled, offers good opportunities for detecting variation. One study found low transitiveness while comparing somatic incompatibility and RAPD markers in *S. granulatus* (Jacobson et al. 1993). Other findings suggest that somatic incompatibility and RFLP/RAPD markers can be used independently for studying the genetic structure of populations (Egger 1992; Egger et al. 1991; Bae et al. 1994; Meijer et al. 1994; Guillaumin et al. 1994; de la Bastide et al. 1994). However, genetic variation in ribosomal DNA regions such as the ITS and IGS is usually too low for use in population studies (Gardes et al. 1990; Henrion et al. 1992; Erland et al. 1994).

Correlations between genet distributions obtained by different methods have generally been high for root-rotting basidiomycetes (Korhonen 1978; Kile 1983; Stenlid 1985; Guillaumin and Berthelay 1990; Lewis and Hansen 1991; Guillaumin et al. 1994). Sen (1990) found a good correlation between isozyme analyses and somatic incompatibility in *S. bovinus* and *S. variegatus*. Isoenzymes are routinely used as indicators of genetic structures in plant populations but frequently used in fungi in general and ECM fungi in particular. However, isoenzyme markers are sometimes not sufficiently variable for population analyses (Egger 1992; Zhu et al. 1988; Sen 1990; Keller 1992).

Undoubtedly, DNA methods, such as RFLP markers and RAPD techniques, will make it possible to analyse genetic and spatiotemporal structures of ECM populations that could not be studied before, such as members of the genus *Cortinarius*. The possibility of fingerprinting single mycorrhizal root tips using these techniques is also intriguing. However, in choosing the method to be used for delimiting genets, availability, cost, and the nature of the question being addressed need careful consideration.

Characteristics of genets

Size of genets

The typical size of genets varies greatly between fungal species, from a few millimetres in bark fungi (Brayford 1990) to over a kilometre in tree root pathogens such as *Phellinus weirii* and *Armillaria* (Dickman and Cook 1989; Anderson et al. 1979; McCutcheon and Carroll 1993). The characteristic sizes of different species will vary depending on the type of resource they occur on, ability to produce migratory mycelium, resource availability, and the relative importance of spore establishment and vegetative spread. Known population structures in pathogenic and saprotrophic fungi are summarized elsewhere (Rayner and Todd 1979; Rayner and Boddy 1988; Stenlid 1993).

The first study dealing with the population characteristics of ECM fungi revealed that *Suillus luteus* in a forest stand consisted of several genets, some of which were at least 2 m wide (Fries 1987). The aim of that study was not to measure the sizes of genets, so typical genet sizes in *S. luteus* are likely to be larger. Table 1 summarizes reported maximum genet sizes in ectomycorrhizal fungi. Note that the observed genets only represent the reproductive part of a fungus population visible at the time of study. Intrapopulation variability in mycelial biomass and sporocarp production can result from spatially and temporarily differing soil environmental conditions such as humus moisture, vegetation cover, or intensity of fungivore grazing (Leonard and Anderson 1991). Consequently, to reveal the actual spatial domain, the mycorrhizas and extramatrical mycelia would also need to be considered. However, since such studies are laborious, the most practical measurement is often the distance between the outermost sporocarps within a genet. Based on such measurements, our studies of 10 populations of *S. bovinus* in Sweden, have shown that genets may be up to 20 m in size covering more than 200 m^2, and that there is a considerable variation within the same population (Dahlberg and Stenlid 1990, 1994, and unpublished data). Six populations of *S. variegatus*, all but one located in more than 100-year-old secondary Scots pine forests, have also been mapped using somatic incompatibility (A. Dahlberg, unpublished data). The sizes of genets ranged up to 27 m in diameter. In *S. granulatus*, genets reached up to 20 m (Jacobson et al. 1993) and a study of *Laccaria bicolor* revealed that genets can be at least 12.5 m (Baar et al. 1994). The size of dense hyphal mats of ECM fungi are between 1 and 5 m (Table 1).

These data indicate that spatial characteristics differ between taxa, e.g., mat-forming ECM fungi seem to have smaller mycelial domains than *Suillus* species (Table 1). We predict that the future mapping of population structures in ECM will reveal a strong relation between the spatial characteristics of a given species and its autecology.

ECM fungi do not commonly form fairy rings (Ogawa 1985). However, in cases where they are formed, the rings probably consist of a single genotype. Fairy rings formed by other fungi have always been found to consist of a single genotype (Mallet and Harrison 1988; Dowson et al. 1989).

Fragmentation of genets

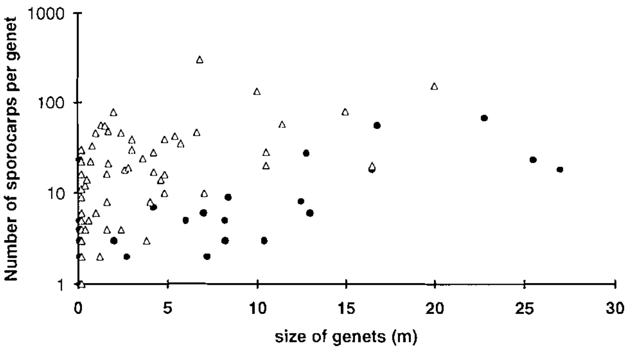
The indeterminate clonal growth pattern in fungi is likely to result in fragmentation of genets into physically and physiologically discrete mycelia, as a result of fungivore grazing, episodes of harsh environmental conditions, etc. (Shaw 1988; Ponge 1991). Fragmentation may also be the result of intrinsic factors; for example, the costs of maintaining bulky mycelial units may be too high. Once a genet is fragmented into ramets, the latter become the functioning units within the population. Although the fragmented mycelia proliferate and expand independently, some may form larger units again by fusing with other ramets within the genet, while others may die. The number of independent mycelial ramets and their degree of integration into larger collaborative units can vary considerably depending on fungivore grazing intensity, soil humidity, and other factors. Single mycorrhizas are in theory capable of independent existence since they constitute the smallest unit that can tap carbohydrates from the tree. It is likely that most ECM genets consist of several independent ramets (Dahlberg and Stenlid 1990, 1994).

Table 1. Estimations of sizes, densities, and ages of genets of ectomycorrhizal fungi as reflected from sporocarps.

Species	Size (m)	Density (ha^{-1})	Age (year)	Ref.
Cantharellus pallens[a]			39+	Jahn and Jahn 1986
Hebeloma crustuliniforme[a]	1.5			Horn 1933
Hebeloma cylindrosporum[b]	—	800–5000		Gryta et al. (unpublished data)
Hydnum ferrugineum[c]	5	65	150+	Hintikka and Näykki 1967
Hysterangium crassus[c]	1			Cromack et al. 1979
Laccaria bicolor[d]	12.5	130–170	16–31+	Baar et al. 1994
Lactarius controversus[a]			36+	Jahn and Jahn 1986
Leccinium aurantiacum[e]			23+	Jahn and Jahn 1986
Russula aurata[a]	7		36+	Jahn and Jahn 1986
Russula olivacea[a]	7–10		33+	Jahn and Jahn 1986
Suillus bovinus[d]	20	30–900	50+[f] (35[g])	Dahlberg and Stenlid 1990, 1994
Suillus granulatus[b,d]	~20			Jacobson et al. 1993
Suillus luteus[d]	2			Fries 1987
Suillus variegatus[d]	27	51–74	70+[f]	A. Dahlberg (unpublished data)

[a] Estimation based on localized production of sporocarps.
[b] Estimations based on RAPD molecular markers.
[c] Estimation based on presence of continuous mycelial mat.
[d] Estimation based on somatic incompatibility.
[e] Estimation based on occurrence of albino sporocarps.
[f] Age estimated assuming a maximal mycelial extension rate of 20 cm · year^{-1}.
[g] Estimated mean life expectancy.

Fig. 1. Number of sporocarps produced by genets in various populations vs. their spatial distribution measured as the maximum distance between the outermost sporocarps. Open triangles, *Suillus bovinus*, 69 genets from five populations (Dahlberg and Stenlid 1990, 1994). Solid circles, *Suillus variegatus*, 45 genets from three populations (A. Dahlberg, unpublished data).



Fragmentation may have a selective advantage since the risk of mortality is spread out among the resulting ramets, thereby reducing the probability of extinction of that particular genet (Cook 1983; Tuomi and Vuorisalo 1989). Fragmentation may also prevent cytoplasmically transmitted mycoviruses from spreading through the mycelium (Brasier 1990). Fragmentation is a common feature in plants (Harper 1977) and probably occurs in most fungi as well. It has been reported in *P. weirii*, *Tricholomopsis platyphylla*, *Armillaria* spp., *Marasmius androsaceus*, and *S. bovinus* (Childs 1963; Thompson and Rayner 1982; Kile 1983; Holmer and Stenlid 1991; Dahlberg and Stenlid 1994).

The ramets proliferate and form sporocarps independently. In saprotrophic fungi it has been suggested that a mycelium needs a threshold biomass to start producing sporocarps (cf. Harper and Webster 1964). By contrast, in ECM fungi, carbohydrate flow from the host is probably the factor regulating the potential for fruiting. In cases where fragmentation has occurred, genet size might be a poor predictor of the vegetative biomass supporting each sporocarp. Our studies comprising over 200 genets of *S. bovinus* and *S. variegatus* indicate that fragmentation is common. Aggregates of somatically compatible sporocarps were frequently found separated by several metres (Dahlberg and Stenlid 1990, 1994). Furthermore, the production of sporocarps of a genet is not proportional to its size (Dahlberg and Stenlid 1994; Fig. 1). In another study, we excavated forest soil, mapped *S. bovinus* mycorrhizas, and identified their genetic identity by somatic incompatibility (Dahlberg and Stenlid 1994). We found that all tested mycorrhizas within the investigated areas (7 and 5 m^2) belonged to the same genet and that they were patchily distributed, as if fragmented.

Longevity of genets

Because of its indeterminate growth habit, a fungal genet should, in principle, be able to live forever if its nutritional requirements are met and external mortality factors are absent. Short roots of trees, the main food resources for ECM fungi, are spatially rather evenly distributed in the forest floor. When short roots die, new ones become established more or less at the same location. Most ECM species in forest systems depend on mycelial spread to colonize new short roots. Such colonization is a prerequisite for maintenance and expansion of mycelial domains (Mason et al. 1987; Newton 1992). If no major disturbance occurs in the forest, mycelia have the potential to survive as long as their host trees, or perhaps even longer. Also, since scattered trees survive moderate forest fires, ECM mycelia are, in general, continuously present in the stands.

Estimated ages of ECM fungi range from 30 to 150 years (Table 1). Among saprotrophic and pathogenic fungi estimates of the longevity of genetically stable mycelia range from 15 to more than 1000 years (Jahn and Jahn 1986; Dickman and Cook 1989; Piri et al. 1990; Smith et al. 1992). Age estimates are often based on spatial genet distributions with an assumed average annual mycelial extension rate (Dickman and Cook 1989; Dowson et al. 1989). Estimates of mycelial growth in ECM range from 2.4 to 5.6 mm · day $^{-1}$ in seminatural conditions to 20 cm · year^{-1} under natural conditions (Read 1991; Dahlberg and Stenlid 1990). However, mycelial extension rates may vary between years as a result of changes in soil conditions and they are likely to be influenced by mycelial size. It is also difficult to estimate the point of origin for genets in ECM species not producing sporocarps in fairy rings. If mycelial growth rate is to be used for age determination it is important to ascertain whether the species exhibit a polarized growth habit. This is not necessarily the case for ECM fungi since as their source of food (fine roots) becomes exhausted, they must move to new fine roots that appear, and such roots can grow out in any direction from old ones. If the growth of a genet is not centrifugal, it would probably be most appropriate to consider the genet as a mobile unit, which may fluctuate in size and location.

In *S. bovinus*, we have tentatively estimated the mean life expectancy of sporocarp-producing genets to be 35 years. Such estimates can be made by comparing population densities at different successional stages, assuming that all genets were established at the same time from a single cohort and that the mortality rates have been constant. These assumptions are probably not completely valid since, in addition to the large genets characteristically present in old stands, we have always found several small genets (Dahlberg and Stenlid 1990, 1994, and personal observations in *S. variegatus*; cf. Hintikka and Näykki 1967). The differences in size imply that the genets differ in age or in their radial expansion rates in soil, or that their spatial domains fluctuate.

There are reports of mycelia of mycorrhizal species producing sporocarps on the same spot for several years, with production being interrupted for 1 or a few years in some cases. Such observations have been interpreted as indicating the presence of perennial mycelia (Augustin 1974; Jahn and Jahn 1986). A convincing case of perennial growth was reported by Jahn and Jahn (1986) who described a mycelium of *Leccinum aurantiacum* that produced albino sporocarps for 23 years. In a study using somatic incompatibility, three populations of *S. bovinus* in 100-year-old forests were followed during 3 successive years (A. Dahlberg, unpublished data). Genet identities of sporocarps were determined based on their somatic incompatibility reactions, keeping cultures of the isolated genets from year to year. Most genets produced sporocarps every year. A few genets produced sporocarps for only 1 or 2 years; sometimes the 2 years of production were separated by 1 year of rest. Using mating tests and RAPD analysis, genets of *L. bicolor* have shown to persist at least 3 years (Buschena et al. 1992; de la Bastide et al. 1994).

Characteristics of populations

Populations can be characterized in various ways. Priority should be placed on spatial and temporal structures, as well as the course of establishment, growth, and death of component genets. The genetic structure of populations may be used to infer historical and evolutionary events such as fluctuations in population size. The genetic structure may also give information on relationships between populations and the degree of gene flow among them.

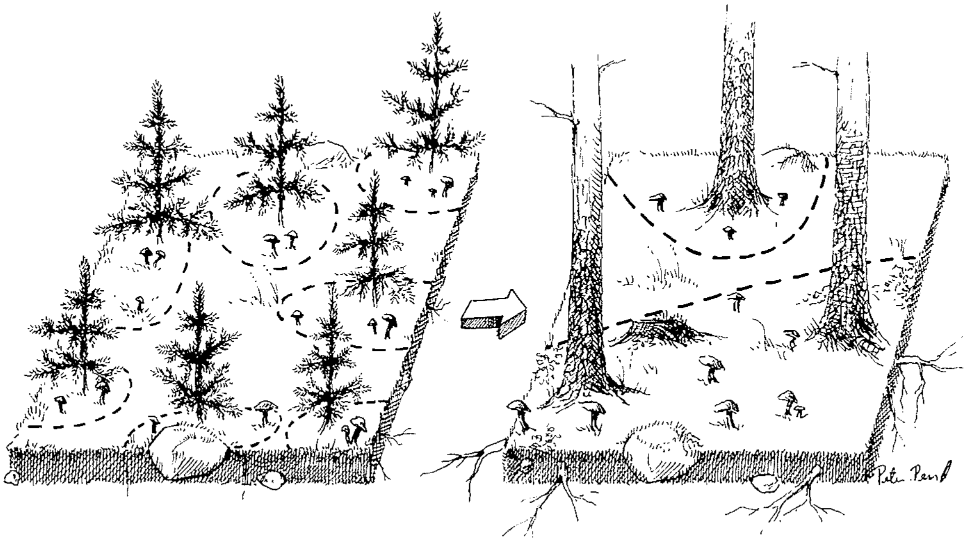
Establishment

Establishment success depends largely on whether the ECM community is open or closed. In an open community there are ample opportunities to colonize vacant fine roots, whereas in a closed community nearly all such sites are occupied. In the open community ruderal traits such as high spore production will afford a selective advantage. Once the community has become closed, the importance of intra- and inter-specific competition as determinants of establishment success increases.

The potential for establishing mycorrhizas from spores is high as exemplified by *S. bovinus* in Swedish forests. Calculations based on an assumed mean production of 10^6 spores · g^{-1} ECM sporocarp dry weight (Dahlberg and Stenlid 1994) and an average production of sporocarp biomass in Fennoscandian boreal forests of about 1 kg · ha^{-1} annually indicate that about 10^5 spores · m^{-2} are produced. The high potential for colonization via spores within a forest is further reflected in the results of experiments with potted seedlings placed in a forest but kept isolated from the forest soil; within 6 months they had become fully mycorrhizal (Robertson 1954). Seedlings planted in nonforested areas, with no ECM mycelia in the soil (in other words, open communities such as former agricultural land or old sandpits) become colonized through the dispersal of spores of pioneer species of ECM (cf. Dahlberg and Stenlid 1990).

In the closed fungal community in established forests, mycelial colonization seems generally to dominate over spore colonization (Newton 1992). Seedlings planted around older trees end up with about the same fungal flora as the latter, whereas if the seedlings have been cored they tend to be colonized by pioneer species instead. In these closed-forest settings, previously established mycelia have the advantage of benefitting from the carbohydrate supply of the host tree when competing for sites on new fine roots. Closed communities are therefore likely to be highly resistant to invasion by spores. However, during the lifetime of natural or seminatural forests, disturbances will inevitably occur that provide windows of opportunity for colonization by spores. Such disturbances can be small scale such as the windthrow of single trees, or large, such as forest fires or clear-cuttings, etc. The frequency of windthrown trees in northern Scandinavia is about one tree per 10–20 ha and year (Söderström and Jonsson 1992). Tree gaps resulting from windthrow, insect attack, or pathogenic fungi can constitute over 30% of the area of a stand but usually account for between 2 and 20% (Quinghong and Hytteborn 1991). In at least some of these gaps, seedlings will become established outside existing mycelial systems and be available for spore colonization. Before fire prevention programs started a century ago in Scandinavia, disturbance caused by natural fire was probably the single most important factor influencing ECM dynamics and succession. The frequency of natural fires in the past varied considerably depending on vegetation type, topogra-

Fig. 2. Generally, young populations of *Suillus bovinus* consist of numerous small genets while genets in older populations tend to be fewer and larger (Dahlberg and Stenlid 1990, 1994).



phy, and region with intervals between fires ranging from about 50 years on dry sediment soils to over 150 years in moist environments (Zackrisson 1977).

Species adapted to small-scale disturbances, such as small gaps, should tend to colonize forests evenly, i.e., in a fine-grade pattern. By contrast, species adapted to large-scale disturbances, such as forest fires, should tend to colonize much larger areas when such are made available, i.e., in a coarse-grade pattern. The episodic spore production of ECM fungi should tend to further reinforce this pattern. It would be interesting to further investigate the degrees to which different ECM fungi respond to small- and large-scale disturbances.

Development of mycorrhizal populations

One likely scenario is that opportunities for fungal establishment are good early in the course of forest establishment but much more limited later on. Following establishment by spores there will be a prolonged phase of mycelial expansion and some genotypes may become extinct. This seems to be true for *S. bovinus*, for which most establishment tends to occur in the early phase. In young Scots pine stands growing in former sand pits, which generally support young fungal populations, the average size of genets was relatively small whereas the population densities were high (Fig. 2). On old forest sites populations were composed of relatively large genets present at low densities.

The initial window for establishment may open later in species that dominate during later stages of forest development than in *S. bovinus*. Accordingly, studies of mycelial domains of *Hydnellum ferrugineum*, which typically fruits in forests 50 – 150 years of age in Fennoscandia, revealed a pattern of small mycelia in young forests and large and small mycelia in older forests (Hintikka and Näykki 1967). This pattern is similar to that for *S. bovinus* although the initiation of fruiting typically starts at a later stage of forest development in *H. ferrugineum*. The same pattern has been observed in the root-rotting basidiomycete *Heterobasidion annosum* (Swedjemark and Stenlid 1993). In this fungus spore establishment is typically in stumps following thinning operations and populations develop by mycelial spread in root systems and the subsequent exclusion of unfavourably positioned genets.

As a population matures the genets will enlarge and grow out from their initial positions. In many of the most successful ECM species outward expansion is accomplished, at least in part, by mycelial cords (Newton 1992). Environmental factors can influence the ability of some species to form cords. For example, an increase in N content of the substrate can adversely affect the growth of extramatrical mycelium of several species (Wallander and Nylund 1992).

Recently, we noted that a changing plant community can influence the development on ECM populations (Dahlberg, Nilsson, and Zackrisson, unpublished data); as the ground cover of *Empetrum nigrum* shrubs expanded under Scots pine on sites where fire has long been excluded, the ECM community shifted over to species that can withstand the allelopathic effects of *Empetrum*. Allelopathic effects on ECM fungi have also been reported by Rose et al. (1983) and Cote and Thibault (1988).

Density

At the local level, the delimitation of a population may be rather hazardous, since natural boundaries are often uncertain. Most species seem to have patchy distributions, since the area over which conditions are favourable for mycelial growth can vary greatly. Still, to compare different populations it is valuable to calculate the number of genets per unit area. Estimated population densities of ECM fungi range from 30 to 5000 ha^{-1} (Table 1). Densities seem to some extent to be species specific. We expect that species-specific densities will be found in ECM fungi as data on more species become available. Species-specific densities have also been reported for some saprotrophic and wood-decomposing fungi (Kile et al. 1991; Stenlid 1993).

Population genetics

The amount of gene flow among populations can be inferred from their degree of similarity. Because of the vast number of spores produced locally in a population of any ECM fungus, the origin of most genets is likely to be local. Doudrick and Anderson (1989) and Doudrick et al. (1990) found indirect evidence for this when comparing the number of repetitions of mating types between populations. There did not seem to be any difference in frequencies over distances ranging from 5 to 1200 km suggesting that spore sources only affected gross frequencies on a local scale. This agrees well with findings for the root rot fungus *Heterobasidion annosum*, where mating types were repeated locally but to a low degree on a regional scale (Chase and Ullrich 1983; Stenlid 1985, 1994).

Interestingly, a very low level of long distance spore spread may still be very important for maintaining a significant level of gene flow among local populations. Given only one interpopulation migrant per generation, populations would not be able to differentiate locally (Slatkin 1987). The validity of assuming that distinct generations exist is debatable in ECM fungi since overlapping generations possibly are the rule rather than the exception, if indeed the concept of generation is appropriate in indeterminate organisms. A migrant should correspond fairly well with a single spore that, together with any second mycelia, manages to establish a mycorrhizal relationship. Nevertheless, wind-dispersed spores are capable of long distance flights, definitely more than 350 km over open sea (Kallio 1970; Stenlid et al. 1994).

In the future, monitoring of genetic differentiation should be a rewarding realm for ECM research. Population genetic markers such as isozymes or DNA probes should help to resolve the question of whether populations undergo strict local differentiation or exist as interrelated metapopulations (Olivieri et al. 1990). The answer to this question would provide a critical key to the understanding of evolutionary relations in this group of fungi.

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